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FAMILY EQUIDAE

V. EISENMANN

African equids are represented by two genera, *Hipparion* and *Equus*. Both are immigrants whose ancestors evolved in North America.

In Eurasia the biostratigraphical significance of the later equids was recognized long ago: *Hipparion* was considered a strictly Tertiary genus whereas the initial appearance of *Equus* was one of the events used to define the beginning of the Quaternary period. Although the onset of the Quaternary is no longer defined in this way, *Equus* remains an important marker in Europe. Its first appearance is at a number of sites which correspond in age to the NM 17 zone defined by Mein (1975, p. 78); furthermore the Villafranchian stenorine *Equus* material is relatively easy to distinguish from the later caballine species. It is rare for *Equus* and *Hipparion* to coexist in Eurasia (Eisenmann and Brunet 1973).

In Africa, hipparions persist at Pleistocene sites and frequently coexist with representatives of *Equus* in sediments that range in age from 2 Ma (first appearance of *Equus* in Africa) to 0.4 Ma (last appearance of *Hipparion* (Eisenmann 1979c)). In Africa it is less easy to differentiate between early Pleistocene and middle to late Pleistocene species of *Equus* than in Europe, partly because of their overall resemblances to the modern zebras and partly because the African fossil material has been less intensively studied.

During the last twenty years the search for fossil hominids in Africa has resulted in the retrieval of large numbers of other fossil mammals including equids. This has helped greatly to improve our knowledge of African *Hipparion* and *Equus*. However, many equid names appearing in faunal lists should be considered *nomina vana* (e.g. *Hipparion albertense*) while others are used despite the fact that detailed descriptions and comparisons with other species have never been published (e.g. *Equus mauritanicus* and *E. oldowayensis*).

Many outstanding studies have been undertaken on equids, and in particular *Hipparion* (Gabunia 1959; Forstén 1968; Sondaar 1968; Alberdi 1974; Zhegalo 1978). However, the standard references for anatomical investigation of *Hipparion* and *Equus* are still those of Gromova (1949a,b, 1952) whose comparison of the skulls, dentitions, and limb bones of these two genera extends to 140 pages and is illustrated by 50 figures (Gromova 1952). For the systems of measurements used here see Table 5.10 (for the cranium) and abbreviations to tables (p. 195 for the teeth. The system of measurements for the metapodials was described in Eisenmann (1979e), for skulls and teeth in Eisenmann (1979a, 1980b).

Figures 5.1 and 5.2 provide a schematic representation of, respectively, an upper left premolar of *Equus* and a lower right premolar of *Hipparion* showing the most important anatomical features. The most important differences between the teeth of the two genera are as follows. The protocone is nearly always isolated in *Hipparion* upper cheek teeth but never so in *Equus*. Ectostylids are frequent in *Hipparion* lower cheek teeth but very rare in those of *Equus*. In *Equus* lower cheek teeth the mesial arm of the preflexid (not the distal arm as

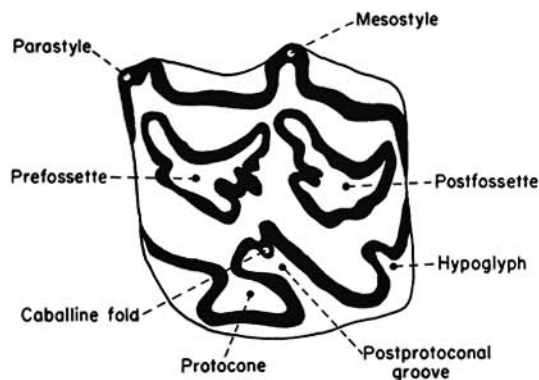


FIG. 5.1. Schematic occlusal view of a left P³ or P⁴ of *Equus*.

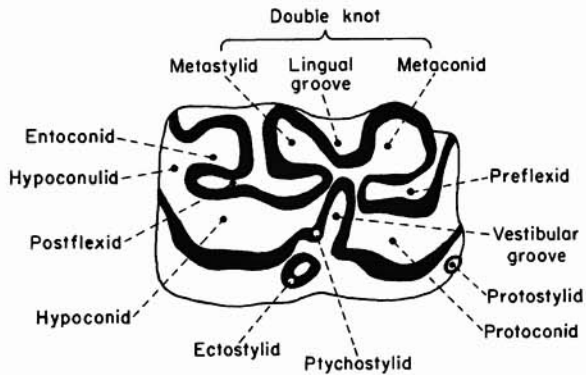


FIG. 5.2. Schematic occlusal view of a right P_3 or P_4 of *Hipparion*.

stated by Churcher and Richardson 1978, p. 402) is usually long and oblique (Fig. 5.3B, arrow), whereas in *Hipparion* both arms are short and directed perpendicularly to the mesiodistal axis (Fig. 5.3D). This feature, described by Gromova, is particularly useful for the identification of *Hipparion* teeth when no ectostylids are present.

Figure 5.3 illustrates the principal shapes of the double knots. In the stenorine type (Fig. 5.3A) the vestibular groove is pointed and narrow; it may be of variable depth. In the caballine type (Fig. 5.3B) the vestibular groove is large and angulated; a similar pattern may be found in some hipparions (Fig. 5.2) which are accordingly said to have caballine or caballoid lower cheek teeth. In the hemionine type (Fig. 5.3C) the vestibular groove is wide, rounded, and shallow, sometimes not very different from the hipparionine type (Fig. 5.3D).

Hipparion De Christol 1832

Diagnosis. Tridactyl extinct equids characterized by isolated protocones on the upper cheek teeth. Many characteristic features of the limb bones are related to the tridactyl mode of locomotion (after Gromova 1952; Sondaar 1968).

Hipparions are not known in Africa until the Middle to Late Miocene. Thereafter, unlike most of the Eurasian hipparions, they persist until the Late Pleistocene, coexisting with species of the genus *Equus* from the Early Pleistocene onwards. Perhaps because of this protracted existence, they have acquired or developed to the extreme some peculiarities: strong ectostylids, caballine double knots and shallow molar vestibular grooves on the lower cheek teeth; reduction of the third incisors; peculiar vomerine morphology and lack of the

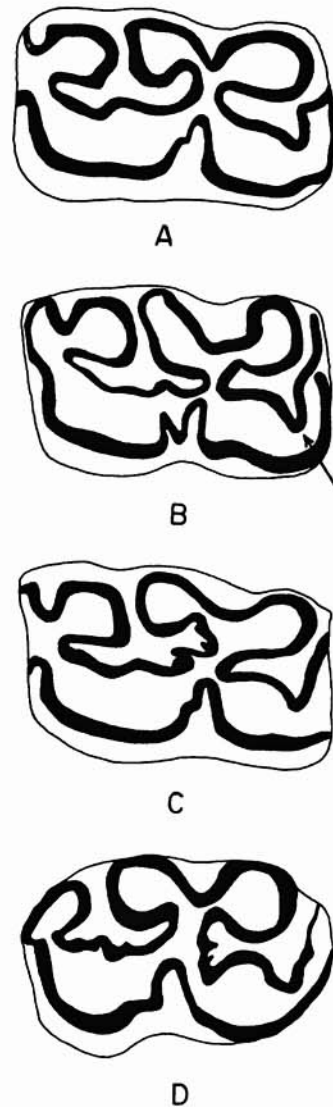


FIG. 5.3. Schematic occlusal views of right P_3 or P_4 ; the pattern of the double knot is (A) zebrine/stenorine; (B) caballine; (C) hemionine; (D) hipparionine.

preorbital fossa in the cranium. Some of these features have motivated the creation of new genera or subgenera: *Eurygnathohippus* (lack of I_3), *Stylohipparion* (well developed ectostylids), *Hypsohipparion* (hypsodont cheek teeth without ectostylids). I believe, however, that our present knowledge of the group is not sufficient to warrant such generic distinctions.

Comprehensive revision of hipparionid taxonomy would ideally require access to samples of good material, i.e. specifically and chronologically homogeneous and representative of the entire

anatomy of the species. At the present only one such sample is known, that of Bou Hanifia (or Oued el Hammam) in the Vallesian of Algeria, which provides a good idea of the nature of *H. africanum*. Most of the other species are based on unassociated material retrieved from sites where two or more species of *Hipparion* may have coexisted. These circumstances lead to endless problems of attribution.

Anatomical features

It seems apparent that *Hipparion* species, like those of *Equus* (Eisenmann 1979a), share many morphological features and intergrade in size. Problems are therefore encountered in positive identification of incomplete material, particularly isolated and upper cheek teeth. As Hooijer and others have stressed on several occasions (Hooijer and Maglio 1974; Hooijer 1975), there are striking similarities between the general pattern of hipparionid upper cheek teeth from sites of 9–12 Ma old (Bou Hanifia, Ngorora) and those from sites of only 3–4 Ma old (Aterir, Kanapoi, Chemeron, Ekora, Usno Formation). Moreover Cooke and Coryndon (1970, Fig. 10) have shown that there is no difference in the length and shape indices of the protocone between Vallesian (Bou Hanifia) and Pliocene hipparions (Langebaanweg and Laetoli). In the first case, however, the upper cheek teeth are associated with primitive 'hipparionine' lowers, unreduced third incisors, and preorbital fossae in the crania, whereas in the Pliocene representatives the same kind of upper cheek teeth are in general associated with 'caballine' lowers with ectostylids, crania lacking preorbital fossa but with a peculiar vomerine morphology and third incisors tending to be reduced or lost (Eisenmann 1976a, 1977, 1979c, 1980a, in press). Let us consider the diagnostic value of these features before discussing any systematic framework.

Cranial features. There is some evidence for interpreting the lack of preorbital fossa as an 'advanced' character. Certainly the four youngest *Hipparion* crania from Africa (Hadar Formation, Koobi Fora Formation, Olduvai Bed II) have none. It must be acknowledged, however, that some of the crania lacking preorbital fossae are more or less contemporaneous with others that possess this feature—crania from Lothagam versus Ekora for example, and perhaps also at Hadar (where some specimens are crushed). Is the presence/absence of preorbital fossae in crania from a single locality an

indication of the presence of two distinct species or lineages of hipparion or merely of intraspecific variation? Another feature of potential importance is the shape of the vomerine part of the cranium. Of the four geologically young crania mentioned above, the two best preserved specimens (Hadar and Koobi Fora Formations) exhibit a peculiar bifurcated vomerine ridge and a very high 'hypercaballine' vomerine index (Eisenmann 1976a, p. 587). Unfortunately crania sufficiently well preserved to show such characters are rare; important as such features may be in theory, they have little practical value.

Upper dentition. The apparent stability of the crown morphology in the upper cheek teeth allows several interpretations. One would be that upper cheek teeth do not change during the evolution of a hipparion lineage; they bear evidence for example, to the direct derivation of the Usno hipparion from the form present at Ngorora. In this case the application of the same specific name to samples from both localities may be justified though perhaps confusing (Eisenmann 1977, 1980a).

A second interpretation would be that the pattern of a tooth varies more or less at random and its differences from or similarities to examples from other localities have no temporal or phylogenetic significance. In effect this would mean that upper cheek teeth were totally useless for specific diagnosis.

A third, more hopeful interpretation would be that some morphological characters of the upper cheek teeth are taxonomically diagnostic but we have not yet found which ones. For example, it is possible that hipparion species might display differences in the respective proportions of individual premolars and molars of the upper tooth row. I have already shown that this is the case with some *Equus* species (Eisenmann 1979a, 1980b)—the interspecific differences are more conspicuous if the pattern of the entire row is taken into account (for example, are protoconal indices of P⁴ greater or smaller than protoconal indices of M¹?). I have begun to look for similar differences in hipparion species but my data are still scanty and lack conviction. Nevertheless, I believe that early hipparions (Bou Hanifia and Nombrevilla) are characterized by only a slight difference in occlusal length between P³ and P⁴ but a greater one between P⁴ and M¹. In contrast, in somewhat younger material from Hadar (c. 3 Ma) P³ is rather longer than P⁴ while P⁴ and M¹ are of similar size. It is also possible that species might be separable on the relative mean size of P³ + P⁴ versus M¹ + M².

Naturally these are presently only working hypotheses which need access to larger samples for verification. With regard to the protoconal indices, the only good monospecific sample I have yet studied is from Bou Hanifia; in this sample the means (calculated on ten more or less complete cheek teeth series) increase from the P² (c. 25) to the M¹ (c. 38) and then decrease via the M² (c. 36) to the M³ (c. 31). Again, access to other hipparion populations is necessary before we can test the taxonomic value of these observations.

Given our present state of knowledge, I do not believe that African hipparions may be diagnosed or differentiated on the basis of their upper cheek teeth. This opinion gains support from the fact that the original diagnostic characters separating the upper cheek teeth of *Hipparion turkanense* from Lothagam from those of *H. primigenium* from Kanapoi and Ekora (Hooijer and Maglio 1974, p. 13) have now been abandoned (Hooijer 1976, pp. 12, 15) although the crania of the two species differ by at least one conspicuous feature—the presence (*H. primigenium*) or absence (*H. turkanense*) of a preorbital fossa.

Incisors. The mandibular symphysis of the type specimen of *Hipparion cornelianum* (originally described as *Eurygnathohippus cornelianus* (Van Hoepen 1930)) is very distinctive—the third incisors are atrophied in contrast to I_{1,2} which are very well developed and crenulated. However, it is difficult to be certain whether or not the reduction of I₃ is a secondary sexual character. Hooijer noted (1975, pp. 30, 36) that there are no canines present in the three known symphyses of *H. cornelianum* (the type from Cornelia and two from Olduvai). A much earlier specimen from the Hadar Formation (AL 177-21) has first and second incisors that are very similar in size and crenulation to *H. cornelianum* but possesses both third incisors and canines (Eisenmann 1976a, Plate 7D). Is this specimen a male (the only known male) of *H. cornelianum* or is it representative of the ancestral stock from which *H. cornelianum* evolved by reducing the I₃ and losing the canine?

Lower cheek teeth. The significance and interpretation of the crown morphology, and that of the ectostylids, of hipparion lower cheek teeth have been discussed elsewhere (Eisenmann 1977). Let us merely say here that for the moment, if one has to deal with only isolated teeth, lower cheek teeth are slightly preferable for identifying and dating African hipparion species. However, even lower cheek teeth are poorly known.

Systematic framework

This would not be the place in which to attempt a comprehensive revision of the African hipparions, even if the all necessary information was available. However, a brief review of the principal taxa that have been recognized on the African continent might be helpful before considering in detail the fossil material from east of Lake Turkana.

Apart from *H. albertense* which must be considered as a *nomen vanum* (Hooijer 1975, pp. 6, 27) and whose lower cheek teeth are not known at all, the African hipparions may be considered in terms of two groups—those in general lacking ectostylids and those in general possessing this feature.

1. *Hipparions in general lacking ectostylids:* *Hipparion africanum* is a middle-sized Vallesian species described (Arambourg 1959) from the relatively rich material of Bou Hanifia, Algeria. The crania possess preorbital fossae; the third incisors are normally developed; the cheek teeth are rather hypsodont, the uppers being moderately plicated and the lowers hipparionine without ectostylids; the limb bones are rather slender (Eisenmann 1980a).

Hipparion primigenium Meyer 1833 is an European Vallesian brachydont species with highly plicated upper cheek teeth, hipparionine lowers with occasional ectostylids and rather robust limb bones. Forstén (1968, p. 14) revised the species and extended it geographically and chronologically to African, Asiatic, and Pikermian hipparions, some of which, like *H. africanum*, are notably different as Forstén herself admits (1968, p. 26, 1978b, p. 307). Hooijer (1975, p. 8) went even further than Forstén by using the name *H. primigenium* for African Pliocene fossils. However, Forstén (1978b) does not appear to confirm these last attributions as she refers only to Miocene *H. primigenium* from Bou Hanifia (Forstén 1972), and Ngorora (Hooijer 1975). In agreement with Sondaar (1971, pp. 438–9, 1974, p. 304), and Alberdi (personal communication) I am afraid that such a broad concept of species may lead to oversimplifications and awkward contradictions.

Unlike the European *H. primigenium*, *H. africanum* has slender limb bones, relatively hypsodont teeth, lowers lacking ectostylids, and only moderately plicated uppers. Some other Miocene African hipparions (Eisenmann 1980a) are larger in size than *H. africanum*, have more robust limb bones and have ectostylids on the lower cheek teeth. Whereas these may be referred to an African form of *H. primigenium*, I see no valid reason to similarly refer the well documented and different *H. africanum*. Too

generalized a concept of species leads to contradictions like the one appearing in the 1978 paper of Churcher and Richardson: in the first column of page 391, *H. primigenium* is said to have ectostylids on the permanent lower cheek teeth, while in the second column of page 393 it is the lack of ectostylids that is mentioned to support the similarities between *H. primigenium* and *H. baardi*. Moreover, if the synonymy between *H. africanum* and *H. primigenium* may be defensible, the use of the name of *primigenium* for Pliocene hipparions with caballine lower cheek teeth is totally confusing; in my opinion the morphology of the double knot is a very important character (Eisenmann 1977) not sufficiently taken into account by Hooijer and Churcher and Richardson.

Hipparion sitifense was described by Pomel (1897, p. 14, Plates I–II) on two upper cheek teeth collected at Saint Arnaud, Algeria; this material is now probably lost. Later on, more material was collected at the type locality (Arambourg 1956, p. 822) and recently described (Eisenmann 1980a; Forstén 1978a, p. 295) but the species remains poorly known: no skull, no incisors, few teeth and limb bones. From the data now available, *H. sitifense* is probably a Miocene species with hipparionine lower cheek teeth lacking ectostylids and moderately plicated uppers; it is slightly smaller than *H. africanum* and may be its descendant (Eisenmann 1980a). The East African Mio-Pliocene and Pliocene fossils referred by Hooijer and Maglio (1974, p. 20) to *H. cf. sitifense* and by Hooijer (1975, p. 22) to *H. ? aff. sitifense* are rather larger in size and at least some have caballine double knots and ectostylids. The relationship between the three forms is not yet clear, nor is the relationship with the small Spanish Turolian hipparions referred by Forstén (1968, p. 33, 1978a, p. 295) to *H. sitifense* (Alberdi 1974, p. 122).

Hipparion turkanense was described from localities of about 6 Ma in age and is characterized by a cranium lacking a preorbital fossa, unreduced third incisors (Hooijer and Maglio 1973, 1974), a relatively high vomerine index (VI = 100 calculated on Plate 1 of Hooijer and Maglio 1974), and a relatively short face (ratio of the projections of the distances between the posterior border of the orbit and the occipital crest and between the posterior border of the orbit and the most anterior point of the muzzle calculated on the same plate = approximately 180). Most hipparions have smaller vomerine indices (Eisenmann 1976a, p. 587) and at least one African hipparion has a much longer

face. Unfortunately the upper cheek teeth are worn and there are no associated lower teeth. Three lower teeth from Lothagam attributed to this species (Hooijer and Maglio 1974, p. 17) have no ectostylids but a fourth one has (Hooijer and Maglio 1974, p. 18). The double knot (or tie) is rather caballine.

The hipparion from the Langebaanweg E Quarry was described by Hooijer (1976) under the name of *Hipparion cf. baardi*. The cranium has a preorbital fossa, a 'normal' vomerine index (VI = 86) and a relatively long face (the index mentioned above is approximately 250 instead of 180 in *H. turkanense*). The size is comparable to that of *H. africanum*. The third incisors are not reduced but the arcade is less rounded than in *H. africanum* and the symphysis is broader, though not as much as in some advanced hipparions (Eisenmann 1976a, Fig. 1). The lower cheek teeth have a morphology intermediate between hipparionine and caballine and lack ectostylids. The same species may be present at Ekora (c. 4 Ma) and was assigned by Hooijer and Maglio (1974, p. 13) to *H. primigenium*. The fragmentary and immature cranium has a preorbital fossa; unfortunately the vomerine index and the length of the face cannot be evaluated. The size of the upper cheek teeth seems comparable at Langebaanweg E and Ekora. The lower cheek tooth found at Ekora lacks an ectostylid (Hooijer and Maglio 1974, Plate 7, Fig. 5) and its morphology is intermediate between hipparionine and caballine. *H. cf. baardi* may be derived from *H. africanum*; in agreement with Hendeby (1978, p. 11), I believe that the E Quarry species is quite different from *H. baardi*.

Hipparion baardi is an appreciably younger species from Baard's Quarry at Langebaanweg, probably about 2 Ma old (Hendeby 1978, Table 5). It has typically caballine lower cheek teeth but without ectostylids (Boné and Singer 1965) and is larger in size. No skull is known.

Hipparion serengetense was described by Dietrich (1942, p. 97) as a subspecies of *H. albertense*, now interpreted as a *nomen vanum*. Though several authors expressed doubts about lower cheek teeth without ectostylids really belonging to an *Hipparion* and not to an *Equus* (Arambourg 1947, p. 306, 1970, p. 94; Hooijer 1975, p. 7), it seems now generally agreed that they do belong to an *Hipparion*. Hooijer (1979) described the teeth collected recently at Laetoli and came to the conclusion that there were in the area two different hipparions: one possessing ectostylids and collected in upper levels, younger than 2.4 Ma, and one lacking ectostylids in levels

about 4 Ma old. Unfortunately the lack of crania leaves it uncertain whether *H. serengelese* (= *Hipparion* sp. Hooijer 1979) is more closely related to *H. turkanense* or to *H. cf. baardi*. The same form with nearly caballine lower cheek teeth seems present at Mpesida and Lukeino (Hooijer 1975, Plate 4 Figs. 4-6; Aguirre and Alberdi 1974, p. 151).

2. *Hipparions* in general possessing ectostylids: *Hipparion namaquense* was described in South Africa by Houghton (1932). The exact locality and horizon are unknown but the teeth are from a single individual. They are very worn and bear very small ectostylids on P_4 , M_1 , and M_2 . The double knot is caballine. The vestibular groove is shallow on the M_3 . Cooke (1950, p. 425) gave the measurements of the row.

Hipparion afarensis from Ethiopia was described in Eisenmann 1976a; it has a cranium characterized by the lack of preorbital fossa, a peculiar vomerine ridge and a very high vomerine index ($VI = 140$); the relative length of the face cannot be estimated. The incisors are large and the third incisors are unreduced. The occlusal length of P^3 is much longer than that of P^4 , that of P^4 is similar to that of M^1 . There are no lower cheek teeth associated with the type cranium; the lower cheek teeth from the Hadar Formation (about 3 Ma old) normally have ectostylids though these are not always well developed (Eisenmann 1977).

Hipparion sp. is another species present in the Hadar Formation. The presence/absence of the preorbital fossa cannot be discussed because the referred crania are either incomplete or crushed; the vomerine index cannot be calculated but the basion-vomer distance is smaller; nor can the relative length of the face be calculated exactly but the face seems long. The muzzle is narrower, with a long and deep gutter on its dorsal face (Eisenmann 1976a, Plate 6, Fig. A). The incisors are notably smaller. The lower cheek teeth are caballine with weakly developed ectostylids.

Hipparion cornelianum (= *Eurygnathohippus cornelianus* Van Hoepen 1930) is based on a mandibular symphysis with I_{1-3} of which I_3 is greatly atrophied. Two similar but more complete specimens were found at Olduvai Bed II and assigned to an hipparion with ectostylids (Leakey 1965, p. 26, Plate 20; Hooijer 1975, p. 26). However, there does not seem to exist a direct association between incisors and lower cheek teeth, which is very troublesome because there is probably more than one species of *Hipparion* at Olduvai (Eisenmann in press).

Hipparion libycum was described by Pomel (1897, p. 8) on the basis of a large lower caballine premolar with a well developed ectostylid collected in the Villafranchian levels of the Carrière Brunie, Oran (Arambourg 1970, p. 92, Fig. 55). The type premolar and the associated fragmentary lower molar are probably lost.

Hipparion ethiopicum (Joleaud 1933) was originally founded on a dozen isolated teeth belonging to different species (and probably different levels) from the Omo deposits (Eisenmann in press). Hooijer (1975, p. 66) selected an M_3 as a lectotype; fortunately the M_3 is associated with three lower molars and possibly one lower premolar of the same individual. These rather large cheek teeth show caballine characters and very well developed ectostylids. The original provenance of the lectotype is unknown.

Hipparion steytleri from the Cornelia deposits (Van Hoepen 1930) is founded upon an upper molar. Lower cheek teeth from this locality resemble those of *H. ethiopicum* but the ectostylids seem more rounded and less developed.

It is conceivable that *H. cornelianum*, *H. libycum*, *H. ethiopicum*, and *H. steytleri* are synonyms but we do not have enough data on the lower cheek teeth to put the last three in synonymy and no certain association between the lower cheek teeth and incisors to put *H. cornelianum* in synonymy with any of the other three species.

KOObI FORA MATERIAL

Hipparion material is apparently not abundant in the Kubi Algi Formation and to date only some 20 specimens have been recovered. A further 60 specimens have been retrieved from the Koobi Fora Formation. Neither sample provides an adequate representation of the several species of *Hipparion* that were present east of Lake Turkana during the Pliocene and Pleistocene—one or two species in the earlier levels and two or three in the upper ones. The samples are, however, sufficient to indicate that there were distinct differences in the assemblages from the two formations and thus render the hipparions useful biostratigraphic zone fossils. As might be expected from the foregoing remarks, some of the material is insufficiently complete to be identified at a species or even a generic level (p. 212). It is also unfortunate that a quarter of the specimens were recovered prior to 1971 and have no certain provenance data.